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When ground-ice replaces fjord-ice

– results from a study of GPS-collared Svalbard reindeer females

SVALBARDS
MILJØVERNFOND

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The Norwegian Polar Institute is Norway's central governmental institution for management-related research, mapping and environmental monitoring in the Arctic and the Antarctic. The Institute advises Norwegian authorities on matters concerning polar environmental management and is the official environmental management body for Norway's Antarctic territorial claims. The Institute is a Directorate within the Ministry of Climate and Environment.

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Preface

The Svalbard Environmental Protection Fund (SMF) has granted the Norwegian Polar Institute (NPI) funds for the project «*Svalbardreinen: til himmels eller på tynn is*?» (SMF 13/60 and 14/115) in autumn 2013 and spring 2014. This is the final report for the project. An international team of researchers from the Norwegian Polar Institute, Norwegian University of Science and Technology (NTNU), Norwegian University of Life Sciences (NMBU), Norwegian Institute for Nature Research (NINA), James Hutton Institute (JHI), Scotland, and the UiT – The Arctic University of Norway carried out the project. To complement the study, researchers from NMBU, NINA and JHI also contributed data and valuable experiences from Nordenskiöld Land, gathered during many years of capture–mark–recapture studies of Svalbard reindeer using GPS telemetry.

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The study complies with current regulations in the Svalbard Environmental Act and the necessary permissions from the Norwegian Food Safety Authority.

Longyearbyen, 15 June 2018

Åshild Ønvik Pedersen
Project leader

A Svalbard reindeer female fitted with a GPS collar. Photo: F. Samuelsson.

Summary

1. Key results

This report presents preliminary results from a four-year capture–mark–recapture study of coastal dwelling Svalbard reindeer, and a comparison with similar data from more inland populations. On Brøgger Peninsula on the west coast of Spitsbergen, there has been a negative population trend since the 1990s due to increasingly frequent rainy and icy winters, while a positive population trend has been evident in central Spitsbergen. We find that the annual home ranges of GPS collared females are smaller in the coastal study populations (Brøgger Peninsula, Sarsøyra and Kaffiøyra) compared to reindeer in the more inland populations on Nordenskiöld Land (Reindalen, Semmeldalen and Colesdalen). The recent lack of sea ice combined with landscape barriers, such as tidewater glaciers and alpine mountains, was predicted to restrict movement among these coastal ranges. Such lack of dispersal opportunities represents a substantial challenge for the reindeer as winter rain and associated ground ice, being much more extensive on coastal compared to inland, are known to trigger an immediate need for increased movement rates and search for better feeding grounds. For comparison, in an earlier period around year 2000, when fjord-ice was relatively frequent and up to one third of marked female reindeer dispersed among the peninsulas, whereas none of the 72 GPS-collared females moved between Brøgger Peninsula, Sarsøyra and Kaffiøyra during 2014–2017. However, for reindeer experiencing restricted opportunities for movement caused by the absence of sea-ice in winter, we observed reindeer adjusting their foraging ecology by an increase in feeding on kelp and seaweed at the sea-shore, as well as foraging on steep slopes high up the mountainsides, where ground-ice is less frequent. Although these responses at small spatial scales may be a strategy to buffer against negative fitness consequences of winter climate change, we conclude that in absence of sea ice may be responsible for the lack of any partial seasonal migration that was observed previously. If the isolation of these coastal sub-populations persist, it may make them less robust to for example extreme stochastic events and the population-genetic challenges of being isolated.

2. Knowledge gain and recommended actions

The project has improved our knowledge of the spatial ecology and behavioural responses to winter climate change of coastal, isolated populations of Svalbard reindeer. Such knowledge of behavioural responses to climate change is of importance to the overall conservation and management of this endemic species. The study also underlines the importance of simultaneously monitoring contrasting reindeer populations (e.g. coast versus inland) to monitor the variation in spatial ecology and population trends. Continued monitoring of these populations together with measures of climatic drivers that lead to poor foraging conditions and isolation in winter, when they are likely to have the greatest need to move, should allow local extinction events to be detected. There are no direct actions to take based on this study, but we recommend that the current overall protection from harvest and relatively low disturbance regime along the coast of Spitsbergen to be maintained.

3. Environmental management implications

The study demonstrates the importance of (1) using GPS collaring as a mean to monitor behavioural responses to climate change, and (2) monitoring several contrasting populations (both coastal and inland) simultaneously, as their responses may differ with respect to changes in environmental conditions. Knowledge of seasonal habitat use is of high importance to the management of the species, and an enhanced knowledge base of the spatial winter ecology is increasingly relevant due to stressors like sea-ice loss and increased human activity). The increased isolation of coastal populations will ultimately make them less robust with respect to stochastic events and genetic isolation, compared to inland populations. Coastal populations are therefore likely to be particularly vulnerable to climate change and increased human activity and disturbance.

4. Follow-up

The winter landscape in Svalbard is changing rapidly, with consequences for populations of reindeer as well as other components of the food web. It will be of great value for management to continue studies of reindeer spatial ecology and fitness in these isolated areas, where changes in winter climate combined with lack of sea ice may affect individuals and populations the most. The management value is especially high when integrated with long-term population monitoring data and in comparison with other (e.g. inland) populations, where the environmental characteristics and the strength of climate effects differ. With the implementation of the *Climate-ecological Observatory for Arctic Tundra* (COAT), it will therefore be essential to monitor both short and long-term consequences of climate change on Svalbard reindeer population and their spatial ecology. This calls for intensive monitoring of Svalbard reindeer population abundances, demographic structure and spatial ecology across contrasting populations combined with monitoring of key drivers affecting these populations, e.g. the timing and extent of sea ice formation in order to quantify the annual degree of isolation in these populations, ground ice, snow depth and hardness.

Keywords:
capture–mark–recapture, rain-on-snow *Rangifer tarandus platyrhynchus*, spatial ecology

Two individually marked female reindeer ready to be released. Photo: Å. Ø. Pedersen.

1 Introduction

The endemic Svalbard reindeer is a key sub-species of the terrestrial high-Arctic tundra ecosystem. The reindeer interact with plant communities through grazing, trampling and fertilization (van der Wal et al. 2004, van der Wal 2006) and provide an important food resource for Arctic foxes (Eide et al. 2005, Eide et al. 2012), and possibly for some polar bears (Iversen et al. 2013). Locally, the reindeer also constitute an important resource for recreational hunting (Pedersen et al. 2014). Internationally, the status of the circumpolar wild reindeer and caribou populations indicates the state of the natural environment (CAFF 2010, Meltofte 2013). Because of this, the Svalbard reindeer is an important species in the ecosystem-based monitoring programme COAT (*Climate-ecological Observation System for Arctic Tundra*; www.coat.no) and MOSJ (*Environmental monitoring of Svalbard and Jan Mayen*; www.mosj.no).

The Svalbard reindeer population on Nordenskiöld Land, central Spitsbergen, has increased over the last three decades (Hansen et al. 2013, Albon et al. 2017). In part, this may be a result of population recovery since their protection in 1925, but it is likely to be more a result of warmer climate with higher biomass production (Vickers et al. 2016) and an extended grazing seasons (Hansen et al. 2013, van der Wal and Stien 2014, Albon et al. 2017). In contrast, some western coastal populations have shown declining or, at best, stable trends in recent years (Hansen et al., in prep.). For instance, in Brøgger Peninsula, the reindeer population size is now about one third of its peak size in 1993, probably in part due to more frequent mild and rainy winters, causing reduced forage accessibility due to ground ice and, thereby, higher mortality and reduced reproduction (Hansen et al. 2011, Stien et al. 2012). Such weather conditions can occasionally encapsulate plants in ground ice and block forage resources for the entire winter season (Putkonen and Roe 2003, Rennert et al. 2009). At the same time, ice on the fjords has become less common (Isaksen et al. 2016, Muckenhuber et al. 2016), which may restrict reindeer from crossing fjords and bays to reach alternative foraging areas (Hansen et al. 2010b, Stien et al. 2010).

The different population trends on Nordenskiöld Land and the western coast indicate that even small differences in climate can be of great importance for reindeer population growth. On Nordenskiöld Land, populations have increased threefold since the total counts started in 1979 (Fig. 1). Since temperatures began to rise in the 1990s, the increase has been around 50 % and is probably related to improved forage resources for the reindeer. The longer and warmer grazing seasons appear to compensate for most likely the negative effects of frequent rainy and icy winters (Hansen et al. in prep., Albon et al. 2017). In contrast, on the north-west coast of Spitzbergen, there is a stronger trend towards much milder and wetter winters, and this may have contributed to the tendency for negative population trends. We do not yet know how this affects the fitness, local movements and migration patterns of the reindeer, but the population in Brøgger Peninsula appears to have stabilized at a much lower level than before the peak in 1993. The current low density and high degree of isolation due to lack of fjord ice may ultimately increase the risk of local extinctions or negative effects of demographic stochasticity, e.g. following extreme events.

The Svalbard reindeer were nearly extinct by the early 20th century, and have been protected since 1925. We know little about the recolonization of the Svalbard reindeer since then (but see Lønø 1959). Emigration to new ranges is probably limited by both high site fidelity, landscape barriers (i.e. glaciers, alpine mountains and open sea) and environmental factors such as fjord-ice conditions (Hansen et al. 2010b), but the importance of those factors may vary across the archipelago. In central Spitsbergen, where valleys are inter-connected by mountain passes at low elevations, the role of landscape barriers and sea ice is likely minor. At the west coast, where glaciers and steep alpine mountains partly block the possibility to move across land, the sea ice likely plays a more important role for the dispersal and spatial distribution of reindeer. For instance, the former presence of sea-ice in Forlandssundet and in Kongsfjorden was likely paramount for the dispersal of Svalbard

reindeer from Brøgger Peninsula (where reindeer were re-introduced in 1978) to the nearby peninsulas, as well as across Kongsfjorden and to Prins Karls Forland.
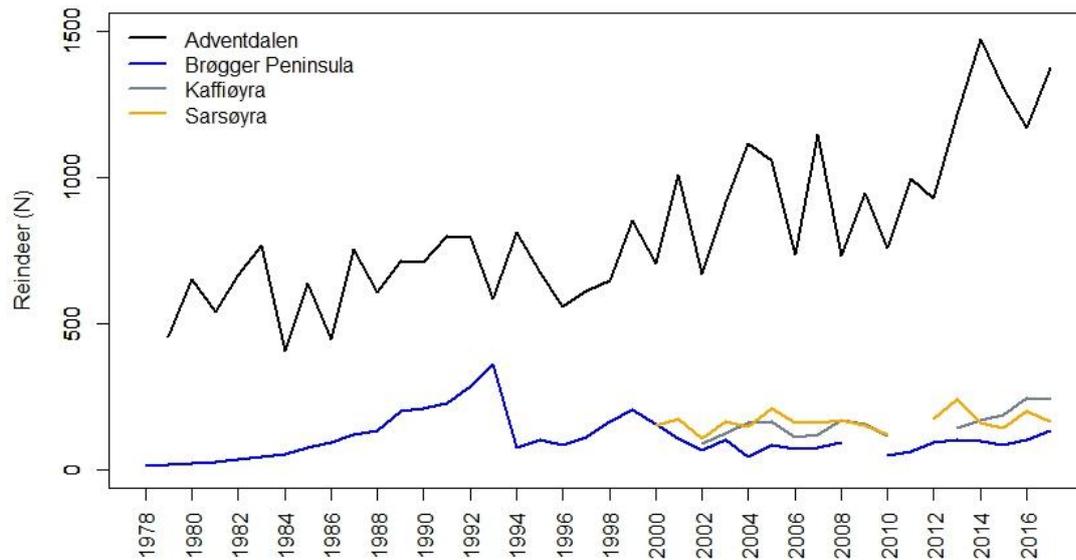

Fig. 1. *Summer population abundance of Svalbard reindeer in Adventdalen (19792017), Brøgger Peninsula (1978–2017; only winter shown on graph), Sarsøyra (2000–2017) and Kaffiøyra (2002–2017) (MOSJ, www.mosj.no; Pedersen, unpublished data).*

Ground icing due to winter rain events triggers reindeer movements (Stien et al. 2010, Loe et al. 2016). The individual motivation for such movements may however vary across Svalbard. Several behavioural responses to icing have currently been described, such as reindeer foraging on kelp and seaweed (despite the risk of diarrhoea (Hansen and Aanes 2012)), foraging at high elevations (despite the risk of avalanches and accidents (Hansen et al. 2009)), and dispersal to nearby ranges (Hansen et al. 2010b, Stien et al. 2010, Loe et al. 2016). Therefore, the interplay between ground ice and fjord ice is likely important for Svalbard reindeer population development and the spatial ecology (Fig. 2).

Objectives

The need to understand how different climate induced effects impact reindeer populations is of high priority in the management plan for Svalbard reindeer (Governor of Svalbard 2009). The aim of this project is therefore to examine how the interactions between changing conditions on land and on sea affect Svalbard reindeer spatial ecology in winter. To achieve this, we performed a capture–mark–recapture study (2014–2017) using GPS collaring of female Svalbard reindeer, examining winter habitat use in the changing tundra landscape at the west coast of Svalbard. We compare these data with historical data from the same study area, as well as data from GPS collared females inhabiting inland tundra landscapes on Nordensköld Land. We also make use of meteorological data, *in situ* snow pack and ground ice measurements to interpret variation in reindeer movement and fitness (body condition, reproduction). The results were evaluated in the context of published/unpublished scientific literature on the topic. By doing so, we were able to address the four main goals of this project:

1. How does absence/presence of fjord ice and ground ice affect body condition, reproduction and spatial behaviour of female reindeer?
2. Can behavioural adjustments counteract climate impacts on forage availability?
3. What triggers and limits female reindeer movement patterns and thereby their spatial distribution?
4. What are the environmental factors driving the different reindeer population trends in Svalbard?
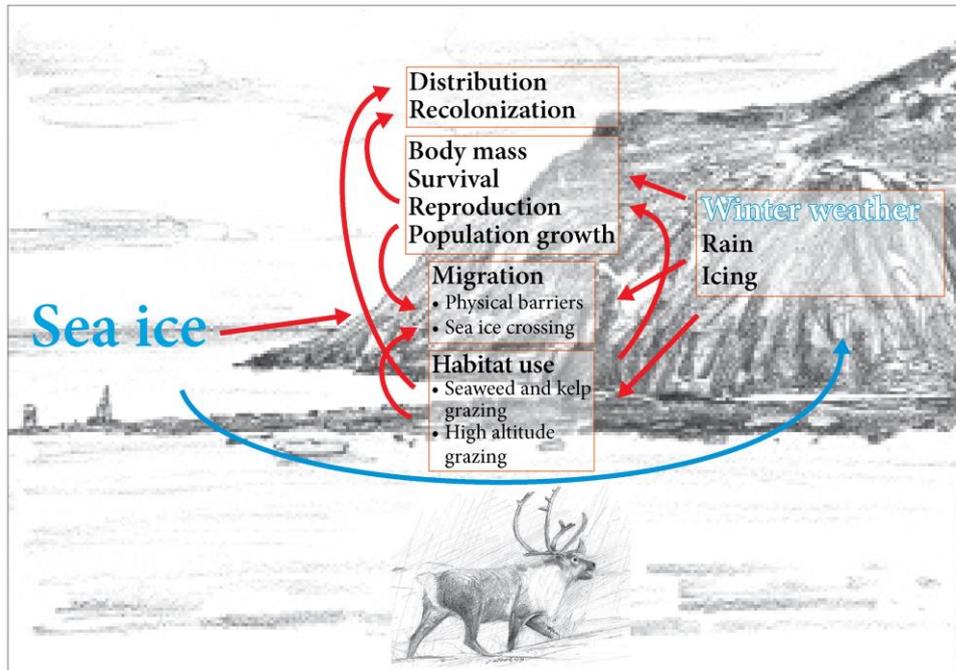
Fig. 2. *A schematic presentation of how changes in fjord ice and ground-ice may affect coastal reindeer populations. Increased winter rain and ground-icing are in part linked to reduced fjord-ice cover. Ground-ice blocks access to vegetation, which can lead to changes in habitat use, but also reduced body mass, survival, fecundity and population growth rate. Ground-ice triggers explorative search for ice-free ranges, which is restricted by increased barriers due to lack of fjord-ice. Lack of fjord-ice also limits the potential for recolonization of new ranges. Illustration: J. Roald, NPI.*

2 Methods

2.1 Study system

2.1.1 Study areas

The high-arctic archipelago of Svalbard (74-81°N, 10-35°E; 62 700 km^2), Norway, comprises 60% glaciers, 25 % barren and sparsely vegetated areas, and only 15 % vegetation covered land areas (Johansen et al. 2012). The study area along the west coast of Spitsbergen consists of three peninsulas, Brøgger Peninsula, Sarsøyra and Kaffiøyra (hereafter collectively termed BSK or coastal populations) (bioclimatic zone C; Elvebakk 2005) (Fig. 3). These peninsulas are dominated by steep alpine mountains, reaching up to 700 m above sea level, with flat open coastal tundra plains in the lowlands. Large tidewater glaciers and fjords separate the peninsulas into three semi-isolated reindeer sub-populations. We compared reindeer data from these coastal populations with data from inland populations in Reindalen, Semmeldalen and Colesdalen (hereafter collectively termed RSC or inland populations) on Nordenskiöld Land (bioclimatic zone B; Elvebakk 2005). Here, the study area consists mainly of three large U-shaped valleys, which are inter-connected by smaller valleys.
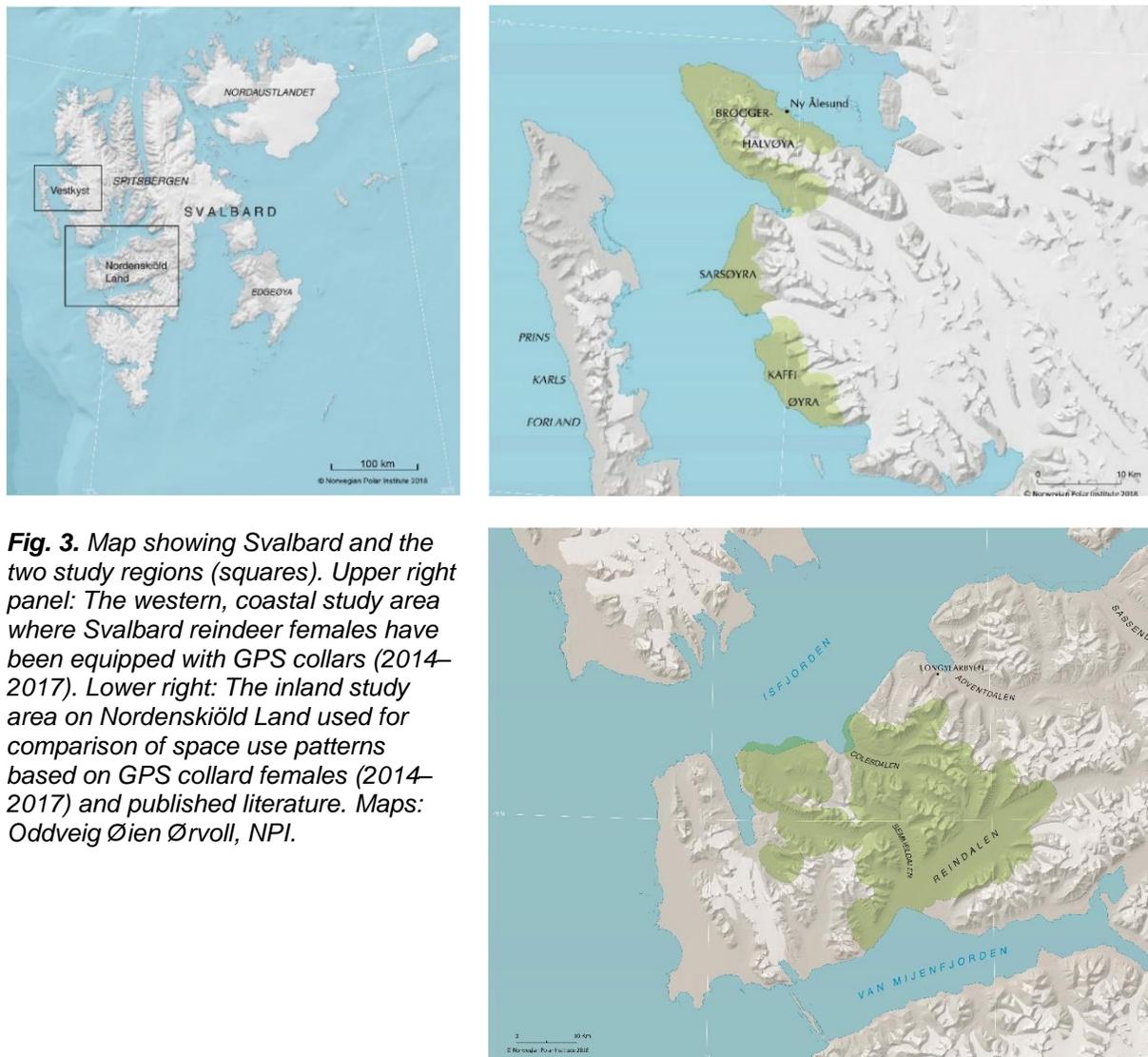
Fig. 3. *Map showing Svalbard and the two study regions (squares). Upper right panel: The western, coastal study area where Svalbard reindeer females have been equipped with GPS collars (2014–2017). Lower right: The inland study area on Nordenskiöld Land used for comparison of space use patterns based on GPS collard females (2014–2017) and published literature. Maps: Oddveig Øien Ørvoll, NPI.*

2.1.2   Study species

The Svalbard reindeer occur in small groups or as single animals year-round (Fig. 4). Unlike many other reindeer, they do not undertake seasonal migrations and appear fairly stationary (Tyler and Øritsland 1989), except in winters with poor feeding conditions (Hansen et al. 2010b, Stien et al. 2010, Loe et al. 2016). Thus, the main driver of seasonal reindeer movements relates to the varying forage availability. Predation on Svalbard reindeer is negligible (but see Derocher et al. 2000) and harvest off-take is low and restricted to certain areas, mostly in Nordenskiöld Land (Pedersen et al. 2014). There is no strong food competition with other large herbivores, or insect harassment. Besides intraspecific competition for food (i.e. density-dependent population regulation), the population growth rates are mainly affected by climatic variability (Reimers 1977, Aanes et al. 2000, Solberg et al. 2001, Stien et al. 2002, Kohler and Aanes 2004, Tyler et al. 2008, Hansen et al. 2011, Hansen et al. 2013, Albon et al. 2017). Parasites are also to some degree found to affect reproductive rates (Stien et al. 2002).

Fig. 4. *The endemic Svalbard reindeer in winter fur. Photo: B. Frantzen.*

2.1.3   Study populations

In Brøgger Peninsula, the Svalbard reindeer was re-introduced in 1978 after being locally extinct for almost 100 years, due to overharvesting. After the reintroduction of 15 reindeer (six males and nine females) from Adventdalen, central Spitsbergen, the population grew fast and reached 360 individuals in 1993 (Fig. 1). In late November that year, large amounts of precipitation came as rain and locked the pastures in ground-ice. During the total winter counts in 1994, only 78 animals were found alive (Aanes et al. 2000, Aanes et al. 2003). Since then, the Brøgger Peninsula population has fluctuated around lower numbers (range [43 – 205]) (Fig. 1). During the 1994 population crash, reindeer from Brøgger Peninsula moved across the fjord ice and established on Sarsøyra, south of Brøgger Peninsula. Thereafter, a population established on Kaffiøyra in 1996–1997 (Aanes et al. 2000). Although movement between these peninsulas can occur at high rates in some winters (Hansen et al. 2010b), it is probably restricted by tide water glaciers and open fjords. The Sarsøyra population increased and was the largest of the three populations until around 2014, after which Kaffiøyra had the largest population (Fig. 1). There is no hunting and very low human activity in these study locations.

In contrast to the coastal populations, several inland populations on Nordenskiöld Land have increased in size since the mid 1990s (Fig. 1; www.mosj.no). In this part of the archipelago, the reindeer can move easily between inter-connected valleys (Loe et al. 2016). There is a low level

of hunting in parts of this area in late August/early September, but otherwise human activity occurs mainly in winter when the landscape can be crossed by snowmobiles.

2.2   Field protocol reindeer capture

We captured female reindeer (adults and calves) in April / May (2014 – 2017) using a handheld net from a pair of snowmobiles, as described by Ormsjø et al. (2009) and Loe et al. (2016) (Fig. 5). Following capture, we manually restrained and handled the animal. We weighed the reindeer to the nearest 0.5 kg and fitted adults (> 1.5 year) with a GPS-collar with satellite-link (Followit, Sweden; 3 positions per 24 h, ca. 12 m positioning error), and calves (10 months of age) with a numbered plastic collar (Fig. 5). All reindeer were also marked with ear-tags. The GPS collar weighs approximately 900 gram (~2 % of the female's winter body weight), while the weight of the plastic collar is less than 50 g. We also collected several types of samples (i.e. blood, pelage hair, ear tissue and faeces). These samples are stored for later scientific use at the Norwegian Polar Institute. In 2014 and 2015, GPS-collars were fitted on adults with unknown age, while collars were redistributed to females with known age (i.e. females previously marked as calves) in 2016 and 2017. The batteries commonly last up to 3 years, but several collars stopped transmitting after approximately 2 years. The reindeer were then recaptured the next season to have the collar removed or the battery changed. Approximately 50 % of the animals were re-captured once, and the individual re-capture rate for the GPS marked females varied between 50–100 %.

Sarsøyra was only accessed twice during the study period, in 2016 by boat and in 2017 by helicopter, due to surging glaciers that hindered winter access by snowmobiles. Kaffiøyra was not accessible in 2016 for the same reason. GPS data and individual based female reindeer data from Nordenskiöld Land were collected every study year according to the same protocol as described above (see also Loe et al. 2016).

2.3   Reindeer data

GPS data: In BSK between 2014 and 2017, 154 Svalbard reindeer (female adults [n=40]; female calves [n=86]; male calves [n=28]) were captured for the first time. In total, 72 animals were recaptured again at least once. Over the study years 82 different individual reindeer females of varying age (≥ 1.5 years) were equipped with a GPS collar (note that not all were used in the analysis due to mortality or low number of fixes). In a given year the total number of active GPS transmitters never exceeded 30 in BSK. Table 1 gives a summary of the number of animals marked by year and location in BSK during the study period. For comparative purposes we extracted GPS data from a total of 66 individuals of varying age in RSC (2014–2017).

VHF data: For comparison we included historical data from our coastal study area. These data were from 28 VHF-collared adult females from 1999-2000, described in Hansen et al. (2010). The data set spanned two summers (July-August 1999 and 2000) and one winter (March-April 2000) of relocations, with positions on average every second-third day. For calculations of annual home ranges, we used only data from 2000.

Population abundance data: We obtained population abundance and calf per female ratios from annual structural population censuses counting age and sex composition in the coastal (www.mosj.no; Pedersen unpublished data) and inland study areas (www.hjorteviltregisteret.no/Villrein/Minimumstelling; Villreinen 2015-2018).

Fig. 5. Upper panel: Capturing of a reindeer with a handheld net from a pair of snowmobiles. Lower panel: Adult female with earmarks and GPS collar (left) and calf with earmarks and numbered plastic collar (right). Photos: F. Samuelsson (upper panel) and Å.Ø. Pedersen (lower panel).

Table 1. Number of marked adult females and calves by study location and year (2014–2017). Female adults were marked either with a GPS collar or a numbered plastic collar. Female calves were marked with a plastic collar, while male calves were only ear-tagged. 'Female adult (GPS collar)' indicates the actual number of females with an active GPS collar in that year, independently of whether the female had the collar on from before, or it was mounted on during re-capture. Brøgger = Brøgger Peninsula, n = total number of reindeer.

Year	Location	Capture event	Female adult (GPS collar)	Female adult	Female calf	Male calf	Total n per study location
2014	Brøgger	First capture	12	-	6	3	21
	Sarsøyra	-	-	-	-	-	0
	Kaffiøyra	First capture	9	1	10	1	21
2015	Brøgger	First capture	-	1	-	1	2
	Brøgger	Re-capture	9	3	-	-	12
	Sarsøyra	-	-	-	-	-	0
	Kaffiøyra	First capture	2	-	6	3	11
	Kaffiøyra	Re-capture	5	5	-	-	10
2016	Brøgger	First capture	-	3	10	2	15
	Brøgger	Re-capture	9	3	-	-	12
	Sarsøyra	First capture	8	-	6	6	20
	Kaffiøyra	-	-	-	-	-	0
2017	Brøgger	First capture	-	-	15	2	17
	Brøgger	Re-capture	9	12	-	-	21
	Sarsøyra	First capture	-	-	16	5	21
	Sarsøyra	Re-capture	12	-	-	-	12
	Kaffiøyra	First capture	4	-	17	5	26
	Kaffiøyra	Re-capture	5	-	-	-	5

2.4   Ground ice and weather data

Ground ice: We obtained data on snow depth and ground ice from the annual measurements in April/early May in the BSK and RSC study systems (see Hansen et al. 2010 and Loe et al. 2016 for details on methodology). Snow pits were dug manually using a spade and, when ground ice was present, an axe or drill was used to penetrate through to the interface with the vegetation/soil. Sampling was conducted annually at the same GPS-locations, which were spatially structured following a hierarchical block design. At the smallest scale, sampling was done on a ridge and sub-ridge about five meters apart (5 m scale) to capture important reindeer foraging habitats. This was repeated twice at a 50 m scale, once or twice again at a 500 m scale, and once at low and high elevation (total of 12 or 16 pits in one transect spanning an elevational gradient). Each block of 16 snow pits was repeated at eight different locations across RSC (total n = 128 pits), and at two locations on the southern and northern part of Brøgger Peninsula (total n = 40 pits).

Meteorological data: We obtained daily data on temperature and precipitation from Svalbard Airport and Ny-Ålesund weather stations using the Norwegian Meteorological Institute web-based services (eKlima). We considered daily precipitation as rain when mean daily temperatures ≥ 1 ° C (see Hansen et al. 2013).

2.5 Data analysis

For all statistical analyses, we used the statistical program R (R-core team 2018).

Annual and spatial variation in body mass: We ran linear-mixed effects models using the 'lmer' function (R package 'lme4', Bates *et al.* 2015) to analyse fluctuations in body mass (i.e. the response variable). This modelling approach is recommended when analysing replicated data, i.e. re-capture of the same individual over several years (Zuur et al. 2009). The random intercept structure (variation in mean between replicated units) was composed of individual, population and/or year. Mean estimates and associated 95 % confidence intervals were obtained by including the following fixed effects: 1) year × age for estimating annual age-specific body masses (adult or calf); and 2) area × age for estimating annual body masses per population, divided by age categories. Factors included as fixed effects were excluded from the random intercept structure described above.

Annual home-range estimation: We used positional data for each of the GPS-marked female in the study areas to estimate annual home ranges. Prior to the spatial data analysis, we removed unrealistic outlier positions by following the protocols and thresholds for screening variables of Bjørneraas et al. (2010). Likewise, we used the positional data for the VHF animals (n=28) to calculate annual home-ranges (but keep in mind that most of the year, the animals were not tracked and the data are therefore not directly comparable to the GPS data) based on tracking in July/August (2000) and in March/April (2000).

We used the 'adehabitat' package implemented in R for calculating annual home ranges using the minimum convex polygon method (MCP) (Calenge 2006). Home ranges were calculated by calendar year. Also, prior to calculating summary statistics for the female home ranges, we removed the data from: 10 females due to mortality or GPS failure from BSK, 3 females from RSC and 2 VHF marked females from Brøgger Peninsula in 2000. Table 2 shows the final number of GPS females (i.e. 135 individual animal years) available per study location for home range analysis. The selected home range estimator, MCP, is a rather crude way to estimate space use, but we selected this estimator to ease comparison with the data from 2000 with fewer re-locations.

Net displacemen: Based on the individual female reindeer positional data, we calculated average net displacement (km) for each animal during the winter period spanning 1 November to 31 March using the function 'ltraj' in the R package 'adehabitat' (Calenge 2006). Net displacement is here calculated based on consecutive positions and distances between them.

Table 2*. Number of females with GPS data suitable for home range analysis available by study year (2014–2017).*

Year	Brøgger Peninsula	Sarsøyra	Kaffiøyra	Nordenskiöld Land
2014	10	0	9	20
2015	9	0	7	20
2016	7	6	0	16
2017	4	11	9	7
Total	*30*	*17*	*25*	*63*

2.6 Literature review

To identify studies relevant for Svalbard reindeer spatial ecology in winter, we searched different sources of published literature (peer-reviewed and non-peer-reviewed). We used the following two terms as search statements - 'Svalbard reindeer' and/or '*Rangifer tarandus platyrhynchus'*.

1. The ISI Web of Science (http://apps.webofknowledge.com, 1945-2017; accessed 4 January 2018; *Rangifer tarandus platyrhynchus* = 148 identified studies). Further, we restricted the searches by using the search statements 'diet', 'habitat', 'spatial' and 'winter' to obtain relevant studies.
2. The peer-reviewed journal *Rangifer* (http://septentrio.uit.no/index.php/rangifer; 1981-2017; accessed 4 January 2018; Svalbard reindeer = 32 identified studies; *Rangifer tarandus platyrhynchus* = 23 identified studies).
3. The Norwegian library system BIBSYS-Brage (https://brage.bibsys.no/xmlui/; accessed 4 January 2018; *Rangifer tarandus platyrhynchus* = 592 identified studies).

In addition, we included information from three manuscripts, which currently are under development by the authors of this report. In Table 3, we have summarized studies that strictly deal with winter spatial ecology of Svalbard reindeer, including winter habitat use and diet.

Table 3. Summary of identified studies, sorted by study type, of Svalbard reindeer spatial winter ecology relevant for the objectives of this report. ISI web of knowledge (login.webofknowledge.com); BIBSYS-Brage (brage.bibsys.no/xmlui/); Rangifer (septentrio.uit.no/index.php/rangifer).

| Study type	Main methods	Main findings	Source	Reference
Winter diet related to forage access	Surveys of feeding craters, snowpack measurements	Snowpack depth and hardness determine reindeer feeding behaviour and diet quality during the winter season.	ISI web of knowledge	Beumer et al. (2017)
Winter diet	Species composition in rumen samples	Graminoids, *Salix Polaris* and mosses dominate the winter diet. In early winter, the diet was a function of plant availability and plant quality, while later in the winter restricted forage availability influenced dietary composition.	ISI web of knowledge	Bjørkvoll et al. (2009)
Winter diet related to forage access	Population censuses and ground ice measurements	13% of the total population were feeding on washed-up kelp and seaweed on the sea-ice foot during an icy winter.	ISI web of knowledge	Hansen & Aanes (2012)
Winter diet related to forage access	Vegetation analyses in feeding craters, snowpack- and ground ice measurements	Some reindeer responded to icing by climbing in steep mountains, others aggregated in the lowlands where they chose feeding craters based on smelling the vegetation beneath the snowpack in ice-free micro-patches.	ISI web of knowledge	Hansen et al. (2010 a)
Winter space use related to forage access	VHF collared females, vegetation measurements	The selection of winter habitat is based more on quantity than quality when forage abundance is reduced due to overgrazing	ISI web of knowledge	Hansen et al. (2009)
Partial seasonal migration	VHF collared females, vegetation measurements	Reindeer on the coast migrated on a seasonal basis among peninsulas (probably on the fjord ice), with improved calving success compared with residents.	ISI web of knowledge	Hansen et al. (2010 b)
Winter space use related to forage access	GPS collared females, ground ice measurements, temperature loggers	Movement among valleys in Nordenskiöld Land occurred in icy winters, and from icy valleys to less icy valleys, resulting in lower over-winter body mass loss, lower mortality rate, and higher subsequent fecundity compared with residents in the departure valley.	ISI web of knowledge	Loe et al. (2016)
Winter space use related to forage access	Satellite collared females and meteorological data	Rain-on-snow events caused an immediate increase in female range displacement and migration to other peninsulas.	ISI web of knowledge	Stien et al. (2010)
Annual and seasonal home ranges and movements	VHF collared females	Female reindeer use small, seasonal summer home ranges.	ISI web of knowledge	Tyler & Øritsland (1989) [1]
Winter space use related to forage access	GPS collared females, ground temperature measurements	Winter home ranges were larger than summer home ranges. Home ranges were larger in winters with ground ice.	BIBSYS-Brage	Kinck (2014) [2]
Seasonal activity patterns	GPS collared females	During winter, activity was at its highest at low temperatures, but decreased with increasing wind speed. During precipitation, reindeer always reduced activity.	BIBSYS-Brage	Kolloen (2015) [2]
Winter space use related to forage access	GPS collared females, ground temperature loggers, ground ice measurements	Reindeer responded immediately to icing by increased movement rates and by increasing the size of their winter home range. Some reindeer moved rapidly closer to the coastline and, as a more delayed response, to higher elevations.	BIBSYS-Brage	Nedberg, (2012) [2]
Winter space use related to forage access	GPS collared females, ground ice measurements	41% of females changed movement strategy when facing icy conditions. In ice-free winters, they remained stationary.	BIBSYS-Brage	Meland (2014) [2]
Body mass and spatio-temporal weather variability	GPS collared females, meteorological data, snow model predictors	April body mass decreases with increasing amount of snow in their used habitat in the preceding October.	BIBSYS-Brage	Movik (2018) [2] [*]
Winter space use and diet related to forage access	Population censuses, fecal stable isotopes, ground ice measurements	Coastal reindeer populations are more likely to feed along the shoreline by ingesting kelp and seaweed on icy winters.	Manuscript	Hansen et al. [3]
Winter space use related to forage access	Population censuses, ground ice and snow hardness measurements	Coastal reindeer populations are more likely to move to high elevations in winter with poor feeding conditions.	Manuscript	Pedersen et al. [3]
Effects of climate on spatial population dynamics	Population censuses, meteorological data	Climate causes large-scale spatial synchrony among reindeer populations, but spatial heterogeneity in both climate trends and responses to climate drivers causes diverging population trends (Adventdalen [inland] versus Brøgger Peninsula [coast]).	Manuscript	Hansen et al. [3]

1) Not listed in ISI.
2) Master thesis; * not listed in BIBSYS-Brage at the time the search was performed.
3) Manuscript that are in preparation and not published by date. Authors and titles are listed as follows: Hansen et al. a) *A salty last resort? Climate change triggers marine biomass ingestion by high-Arctic island reindeer;* Hansen et al. b) *Population synchrony in high Arctic wild reindeer;* Pedersen et al. *Spatial heterogeneity in a correlated environment;* Pedersen et al. *Sea or summit: wild reindeer foraging responses to a changing high-arctic winter.*

3 Results and discussion

3.1 Climatic conditions, ground ice and fjord ice

During the study period (2013/14 – 2016/17), winter temperatures were generally lower in the coastal study region (Ny-Ålesund weather station) than in Nordenskiöld Land (Svalbard Airport weather station) (Fig. 6 a-b). The lower average winter temperature also included lower heat sums, i.e. accumulated temperature above zero or 'degree-days' (Fig. 6 b). Precipitation was also higher in the coastal study region than in Nordenskiöld Land (Fig. 6 c). Furthermore, a higher proportion of precipitation came as rain in the coastal study region. The number of days with rain-on-snow (ROS) increased progressively over the four years in both study regions (Fig 6 d).
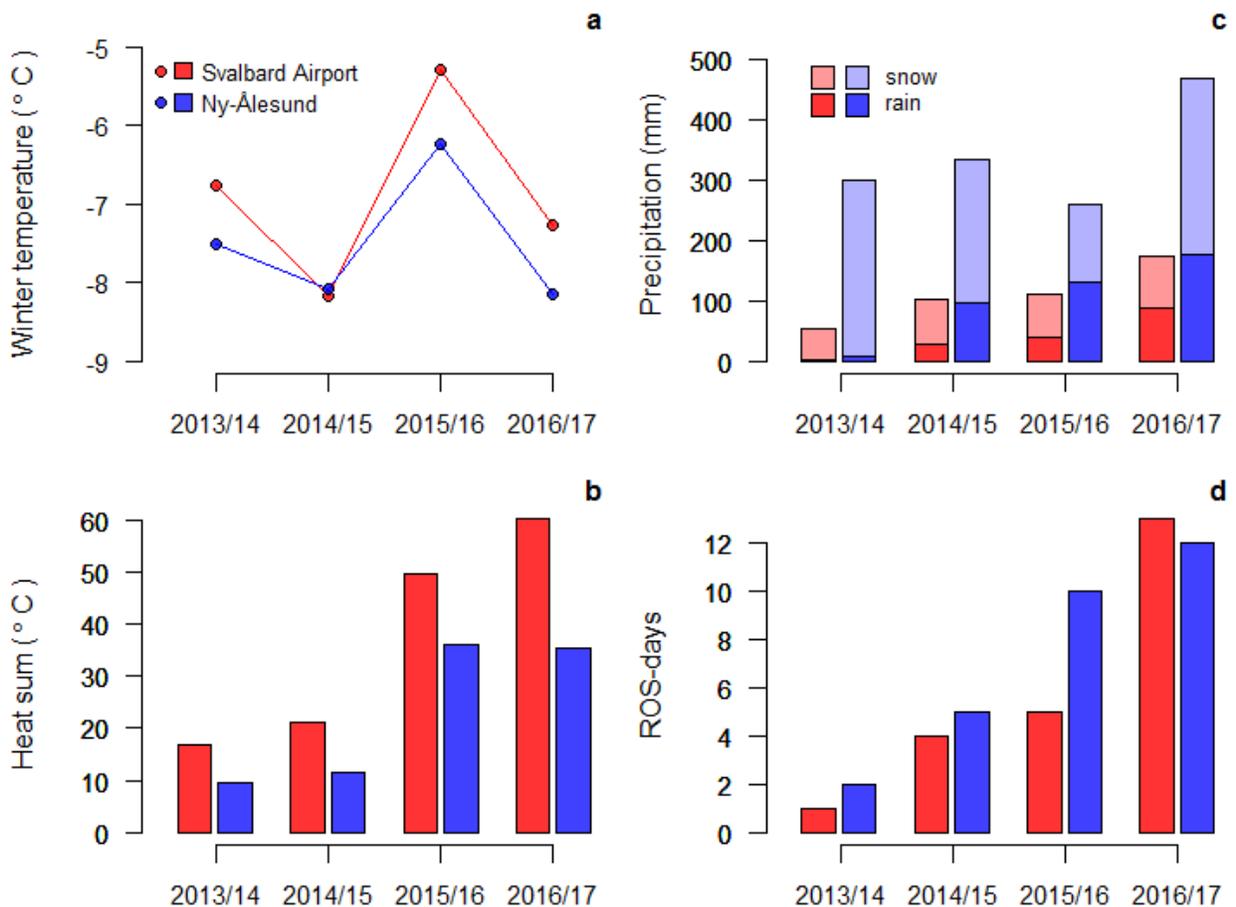

Fig. 6. *Winter climate data (November 1 – March 31) for weather stations at Svalbard Airport (red) and Ny-Ålesund Airport (blue). **a)** Mean winter temperature; **b)** annual precipitation (mm) as rain (dark blue/red) or snow (light blue/pink); **c)** heat sum i.e. sum of degrees above zero; and **d)** number of days with rain-on-snow (i.e. days with precipitation when the temperature is above 1 degree C.*

Across all study years, the mean ground ice thickness was higher in the coastal region than the inland region (Fig. 7 a). There was little ground ice in the winter 2013–14, when there was almost no rain (Fig. 6 c; Fig.7 a). Although the amount of rain and days with ROS increased year-by-year (Fig. 6 c-d), at BSK the thickness of ground ice was highest in 2014–15. A ROS-event in late winter will thus likely result in a thicker ground ice layer than an early ROS-event, because of a deeper accumulated snowpack (Peeters et al. in prep.). The heaviest ROS event in the winter of 2016–17 was in early/mid-November, which may explain why ground ice thickness was less than in 201415 (Fig.7 a). Nevertheless, ground ice formation during ROS-

events is a complex process that not only depends on the amount of rain and snow depth, but also variation in air and soil temperatures during and shortly after the warm spell. Accordingly, if the soil surface is deeply frozen, this may lead to rapid freezing of rain falling on the ground (or percolating through the snow) during a warm spell, particularly when air temperature remains close to zero or decreases quickly after the event. Conversely, if the soil surface is not yet deeply frozen (a situation which may now occur increasingly often in late autumn), ground-ice is less likely to build up.

The mean snow depth was similar in the two study regions (Fig. 7 b), except in 2014 when there was a snow record in Ny-Ålesund. No female was recorded with a calf during the subsequent summer counts in Brøgger peninsula, indicating that snow depth can play an important role, just as ground ice, in shaping the reindeer population dynamics.
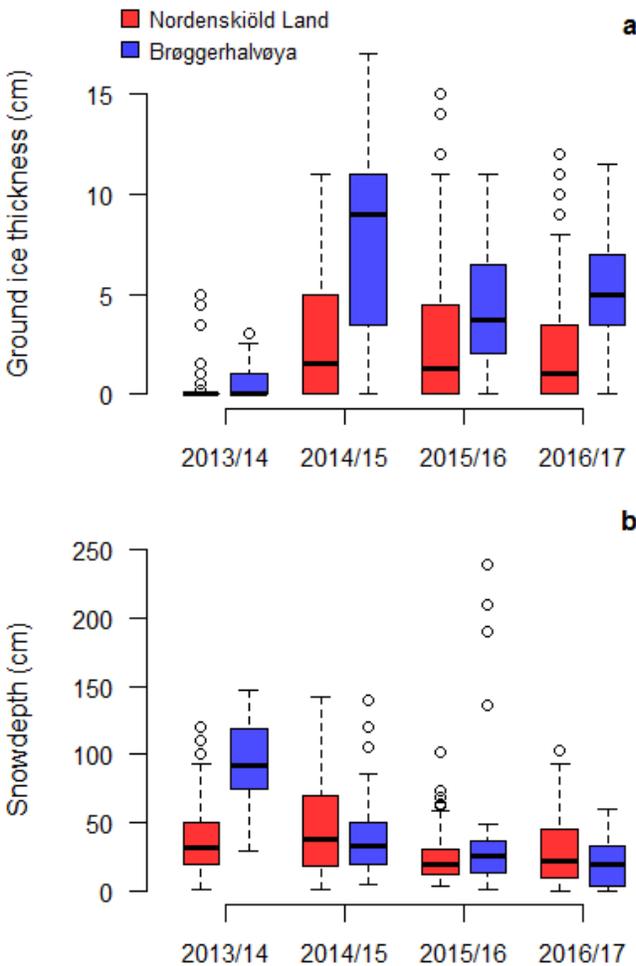
Fig. 7 a) *Annual ground ice thickness (cm) and* *b)* *snow depth (cm), observed in April/early May. Red = Nordenskiöld Land (n = 128), blue = Brøgger Peninsula (n = 40).*

During the study period (2014–2017), there was no fjord ice in any of the bays (Engelskbukta and Hornbækbukta) between the coastal study areas or in Kongsfjorden and Forlandssundet. Thus, the entire study period was characterized by lack of fjord ice suitable for reindeer movement between the coastal study peninsulas.

3.2 Annual and spatial variation in reindeer vital rates

Because of few study years (2014–17), it was not feasible to relate annual measures of reindeer body condition (e.g. body mass) and reproduction statistically to annual variation in spatial extent of ground ice and fjord ice. In addition, during the study period, there was no winter with presence of fjord ice suitable for females to cross the bays between the peninsulas (i.e. Engelskbukta and Hornbækbukta). However, we provide briefly summary statistics for some vital reindeer rates, i.e. body mass and reproduction (i.e. number of calf per female) for each study year and location (Fig. 8 and 9), put in the context of comparable estimates from Nordenskiöld Land (Albon et al. 2017, Veiberg et al. 2017).

Such parameters are also included as key state variables in the long-term monitoring of the *Climate-ecological Observation System of Arctic Tundra* (COAT) and necessary to allow analyses of the relationships between reindeer performance (survival and reproduction) and weather/climate variability on short and long-term temporal scales. When the time series from our study area becomes longer, we will be able to conduct similar analysis as Albon et al. (2017) have done for the long-term capture–mark–recapture study on Nordenskiöld Land, for then to compare estimates.

3.2.1 Body mass

April adult body mass in the coastal BSK study areas, over 2014–2017, fluctuated widely (from 44 [42:47] (mean [95 % confidence interval]) in 2014 to 59 [56:62] kg in 2016, Fig. 8). These variations cover the same range of body mass variation measured in the inland RSC study areas (Nordenskiöld Land) over 20 years (1995-2014, minimum = 40 [39:41] kg in 1996, maximum = 57[56:58] kg in 2001, Veiberg et al 2017). Adult body mass tended to be lower in BSK than in RSC, with respective average of 47 [42:52] kg and 50 [41:59] kg (Veiberg et al. 2017), but not significantly with four years of data. In more details, Kaffiøyra had the highest mean body mass comparable to the RSC, while Sarsøyra had the lowest, despite overlapping confidence intervals (Fig. 8). Calf body mass fluctuated with a similar annual pattern as adults in all the three coastal study areas and years.
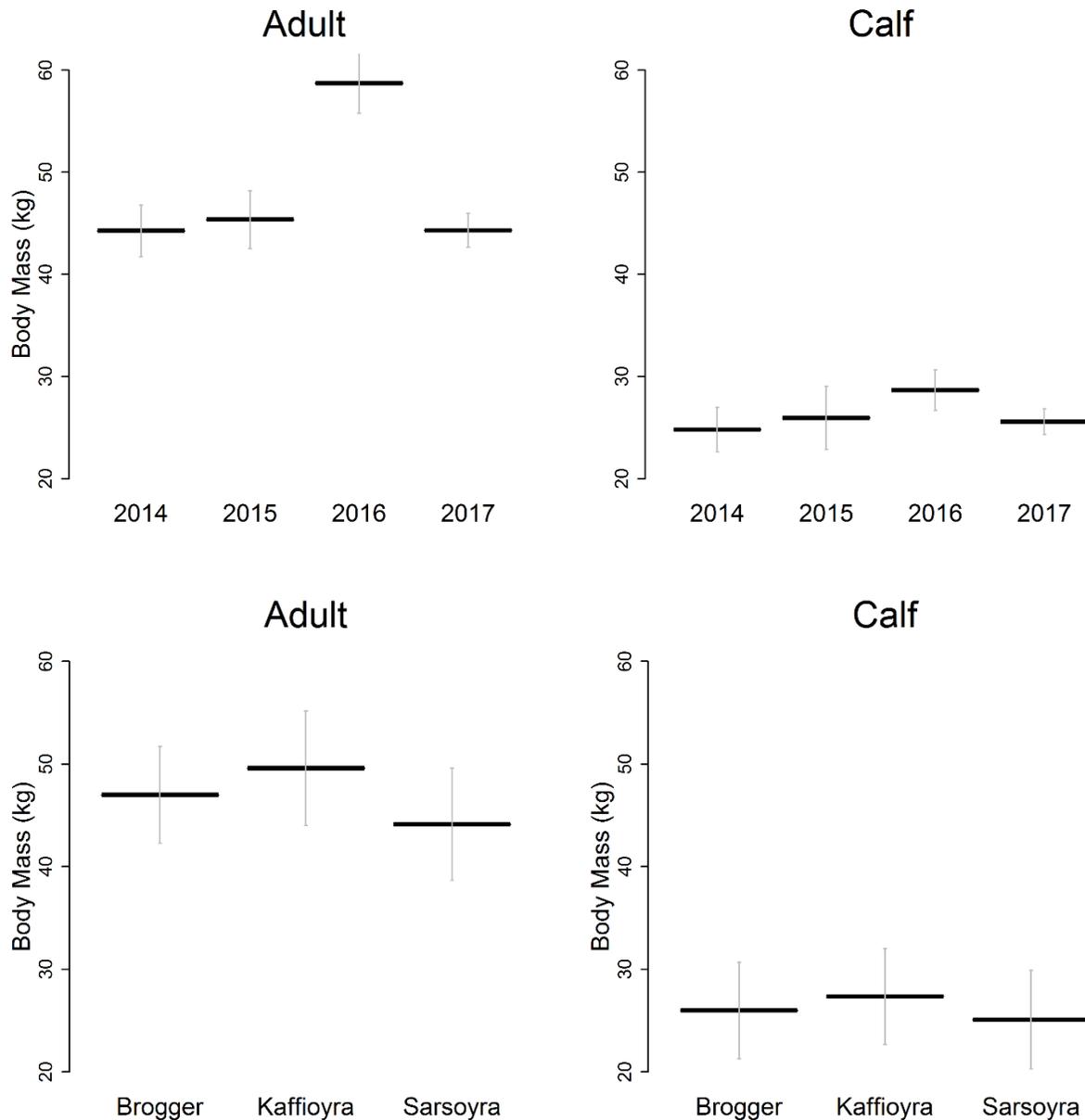
Fig. 8. *Upper panels: Estimated mean body mass (kg) and 95% confidence intervals (grey lines) for adult females and calves by study year. Lower panels: Estimated mean body mass (kg) and 95% confidence intervals (grey lines) for adult females and calves by population, i.e. the coastal study populations Brøgger Peninsula, Sarsøyra and Kaffiøyra. Estimates are obtained from linear mixed-effects models accounting for population (upper panels), and year and individual (lower panels).*

3.2.2 Reproduction

The reproduction rate (calf per female ratio) is determined by maternal winter body mass, in turn largely determined by climate, and in particular winter precipitation (Solberg et al. 2001, Stien et al. 2012, Albon et al. 2017, Veiberg et al. 2017). Accordingly, in 2016, when there had been little winter rain, and no deep snow, and hence fairly high average April body mass, reproduction rates in all of our sites was high. However, in other years, the reproduction rate appeared to vary substantially between the study areas, and even within the adjacent coastal study peninsulas. Despite this overall pattern, reproduction rate on Nordenskiöld Land was more consistent between years (always around ~40-60%) compared to the BSK coastal study areas, which

fluctuated between 0 to 80% (Fig. 9). Furthermore, the local variation within year was much larger in BSK than in RSC. This may indicate that the BSK population is more sensitive to the greater variation in rain-on-snow, icing and other environmental variables including local snow pack depth/hardness and access to alternative forage sources along the shore or at high altitudes, which can differ over small spatial scales in this area.
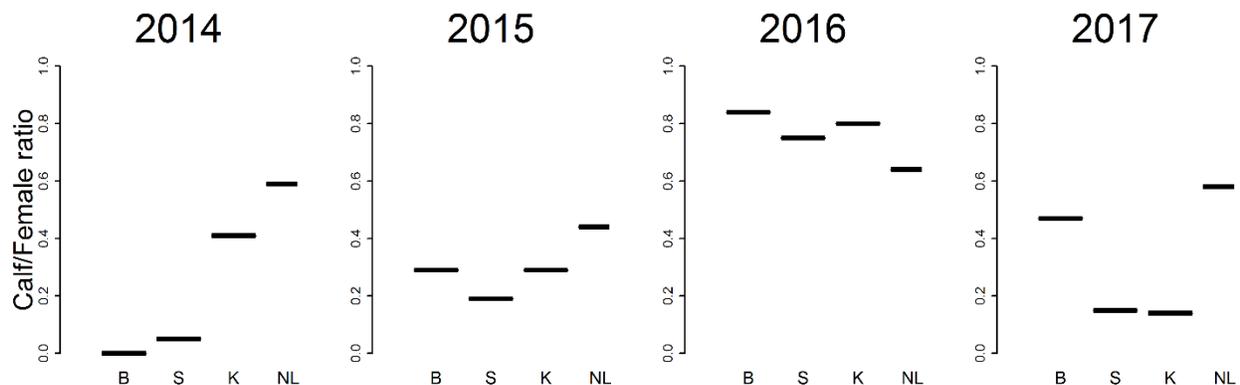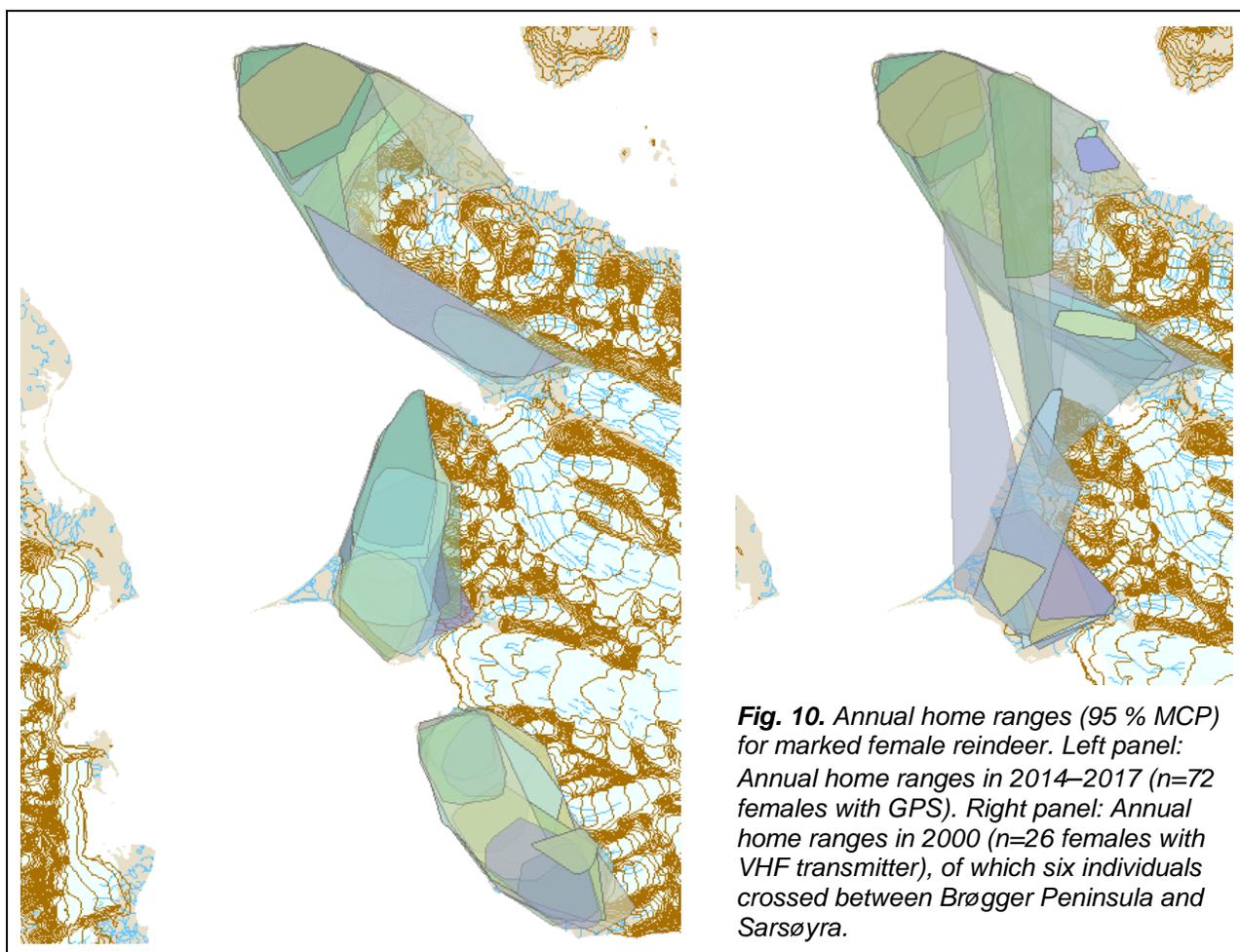

Fig. 9. Number of calf per female observed during the summer structural population survey of 2014–2017 and study location (B = Brøgger Peninsula; S = Sarsøyra; K = Kaffiøyra; NL = Nordneskiöld Land).

3.3 The role of sea ice

During our study period (2014–2017), there was virtually no ice in the fjords or bays surrounding the Brøgger Peninsula, Sarsøyra and Kaffiøyra study locations. Accordingly, no GPS-marked females moved between any of the peninsulas in the coastal BSK study locations. They used more or less the entire peninsulas as their annual home ranges (Fig. 10). Note that we observed that two males marked as calves move between peninsulas among years: We re-sighted one male marked at Brøgger Peninsula (2014) in Sarsøyra in 2015, and another male marked in Kaffiøyra (2015) was resighted in Brøgger Peninsula in 2017. Whether they swam or crossed glaciers remains unknown.

Previous studies of Svalbard reindeer's spatial ecology have indicated the importance of movement corridors in severe winters when pastures are unavailable due to impenetrable ground ice (Stien et al. 2010), or following habitat degradation due to overgrazing (Hansen et al. 2010). In the early 2000s, when fjord ice was more likely to be present as potential movement corridor, 35 % (total n = 34; 1998–2001) of marked females shifted seasonal range between Brøgger Peninsula and Sarsøyra (once or multiple times). Similarly, Stien et al. (2010) demonstrated, based on six satellite tagged females, movement between the two peninsulas due to locked pastures (ground ice) in 1995/96, also a winter with abundant fjord ice. Ground-icing events immediately triggered increased net displacement rates, and one female moved from Brøgger Peninsula to Sarsøyra.

Fig. 10. *Annual home ranges (95 % MCP) for marked female reindeer. Left panel: Annual home ranges in 2014–2017 (n=72 females with GPS). Right panel: Annual home ranges in 2000 (n=26 females with VHF transmitter), of which six individuals crossed between Brøgger Peninsula and Sarsøyra.*

As a likely result of stricter physical movement barriers, including lack of sea-ice corridors, we find that during 2014–17, the annual home ranges were on average significantly smaller for female reindeer in the coastal populations in BSK than the inland RSC (Fig. 10 and 11; Table 4; two sample t-test [t = -4.15, df = 69.62, p-value < 0.05]). This size difference is likely in part also a result of female dispersal events in RSC (Loe et al. 2016), when winter conditions are severe. Also, one might expect the annual home ranges to be smaller in the coastal populations (Brøgger and Sarsøyra) in our study period versus the early 2000s, when some females crossed Engelskbukta and utilized both these ranges. However, this was not evident in the data (Table 4). This could be due to the fact that the two data sets differ with respect to the number and temporal range of positions available (VHF tracking in limited time periods during late winter and mid-summer in 1999–2000 vs. continuous [3 positions per day] positions for 2014–2017). In addition, the difference in home range sizes can be related to changes in feeding conditions. Currently, the coastal reindeer experience milder winters with more frequent ground icing (Fig. 7 a), which likely results in more movement in general, including to higher elevations and to the sea shore for feeding, thus on average increasing the home ranges size.

The lack of sea ice however reduces the possibility to escape severe feeding conditions, especially since these coastal areas are separated by dangerous landscape barriers (glacier crevasses, alpine mountains and large tidewater glaciers). This contrast to reindeer inhabiting inland areas (RSC) with possibilities to move across land to better foraging grounds. The increased isolation of coastal populations may ultimately make them less robust with respect to extreme events and genetic isolation compared to the inland populations in central Spitsbergen (Loe et al. 2016).

Table 4. *Summary statistics for the estimated annual home range size (km², 1 January to 31 December) for GPS collared females in the three coastal study populations (BSK) and the inland study populations (RSC) on Nordenskiöld Land. The table also shows home range estimates for VHF marked females on Brøgger Peninsula for the year 2000. SD = Standard deviation.*

Location	Year	N	Mean (SD)	Median	Range
Brøgger Peninsula	2014–2017	30	34.40 (± 17.47)	30.50	9.37-86.31
Sarsøyra	2014–2017	17	25.44 (± 7.24)	24.57	13.31-25.44
Kaffiøyra	2014–2017	25	25.65 (± 13.18)	22.52	4.20-55.48
Nordenskiöld Land	2014–2017	63	59.3 (± 55.29)	43.23	4.07-281.17
Brøgger Peninsula	2000	26	20.98 (± 21.19)	13.79	2.11-84.14
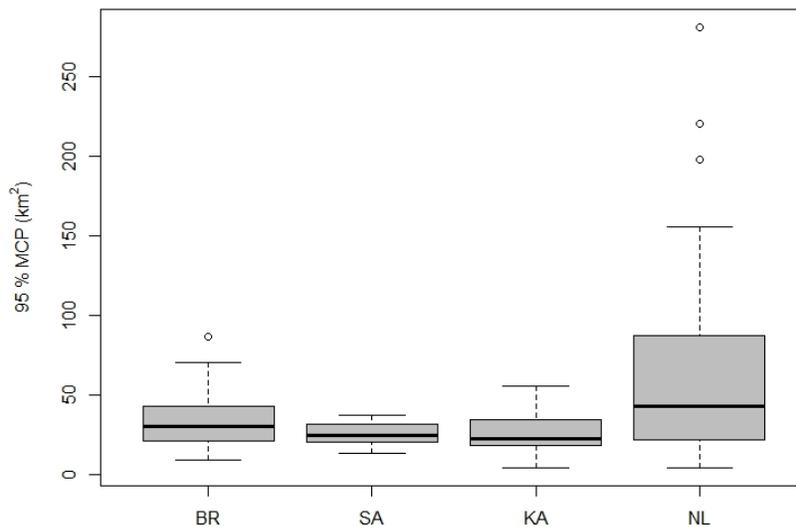
Fig. 11. *Boxplot for the estimated annual home range size (km²) for the study populations with GPS marked females. The black marked line shows the median value, the outer lines of the box show the first and third quantiles, and whiskers show the 5th and 95th percentiles. Extreme values (outliers) are indicated by open dots. BR = Brøgger peninsula, KA = Kaffiøyra, NL = Nordenskiöld Land, SA = Sarsøyra.*

3.4 The role of ground-ice

Reindeer may partly buffer changing environmental conditions by behavioural adjustment. During thousands of years of isolation in a hostile high-Arctic environment, the Svalbard reindeer has developed several strategies to cope with severe winter-feeding conditions. The winter forage availability (Fig. 12) determines the carrying capacity of an area and ultimately the number of animals. Here we give some examples of behavioural strategies adopted in response to increasingly rainy and icy winters, and summarize current knowledge based on literature.

Fig. 12. *Rain-on-snow in winter may result in ground ice, which encapsulates plants in thick solid ice making them inaccessible for herbivores. Photo: L. T. Beumer and Å. Ø. Pedersen.*

3.4.1 Behavioural responses to ground ice: Foraging at the sea-shore

Increased monitoring efforts, longer time series and improved technology such as GPS collars and stable isotope analysis of diets, have resulted in increasing evidence that coastal reindeer use marine food resources to buffer effects of widespread tundra icing. During the population monitoring in the extreme icing winter of 2010, when thick ground ice covered 98 % of the lowlands, Hansen and Aanes (2012) observed that 13% of the reindeer in the coastal populations south of Ny-Ålesund fed on washed-up kelp and seaweed on the sea-ice foot during the population monitoring in late winter (Fig. 13). This probably represents a last attempt to avoid starvation under particularly severe foraging conditions. Recent analyses based on the time series of annual winter population monitoring between 2006 and 2016, along with GPS-collar data and stable isotope analysis of reindeer faeces and their different food sources, now confirm the link between this marine foraging strategy and rainy and icy winter conditions (Hansen et al. unpublished).

### 3.4.2 Behavioural responses to ground ice: Foraging at high elevations

Although some individuals utilize kelp and seaweed, this food source is only present in some areas (and variable among years) and probably needs to be combined with input of terrestrial food. Foraging of kelp and seaweed also appears associated with diarrhoea (Hansen and Aanes 2012). Accordingly, the monitoring data from the coastal populations suggest that most reindeer apply other behavioural strategies to cope with poor winter-feeding conditions. One such strategy, particularly common among adult males, is to move to high elevations and steep mountain slopes where ground ice is less likely (Fig. 16 for an example). Despite extremely low plant biomass at such high elevations (i.e. polar desert), and a substantial mortality risk (see Leader-Williams 1980 for and example) due to e.g. avalanches, we find that up to 50 % of the reindeer in the BSK populations were located in steep terrain above 300 m altitude during some icy or particularly snow-rich years. In favourable winters, no reindeer used this habitat (Pedersen et al. in prep.).

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Fig. 13. Upper panel: A young Svalbard reindeer feeding on washed up kelp and seaweed. Lower panel (left): Feeding craters at the sea-shore at Huklagunene, Kvadehuken, Brøgger Peninsula. Lower panel (right): A male feeding at the sea-shore in March right outside the Ny-Ålesund research base. (Photo: Malin Daase, Å. Ø. Pedersen and L. T. Beumer).

Movement to higher areas after rain events is also found by inspecting the GPS data. To exemplify this strategy, we show here an example from Kaffiøyra, where elevational feeding is commonly observed during harsh winters (Fig. 14). The GPS females (n=9) experienced a rain episode in mid-February (16 February 2015, 20.7 mm [Ny-Ålesund weather station]) and responded by a slight increase in net displacement (Fig. 15 a) and by moving to higher elevations (Fig. 15 b). Interestingly, these individuals experienced an even heavier rain event earlier that year (January 22 and 23, 20.5 and 42.3 mm, respectively [Ny-Ålesund weather station]), and some minor events in early winter, but with no apparent spatial response. One reason for these differences may be that the impact of a rain event on feeding conditions depends on how much snow, as well as ice, has accumulated over the season. The elevational feeding demonstrates a spatial response to worsening winter-feeding conditions with a strong selection for the periphery of the realized foraging niche.
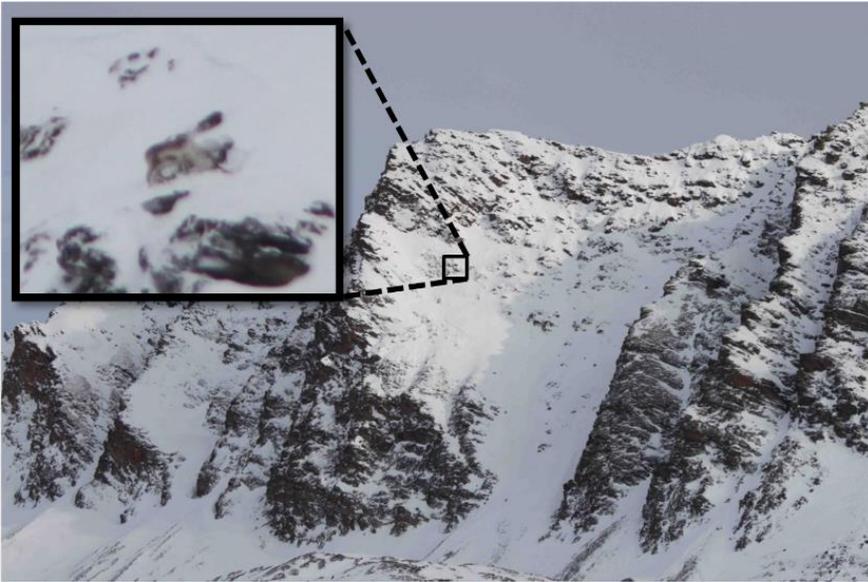
Fig. 14. Svalbard reindeer foraging at high-elevations in steep, alpine mountains along the west coast of Svalbard. Photo: B. B. Hansen.
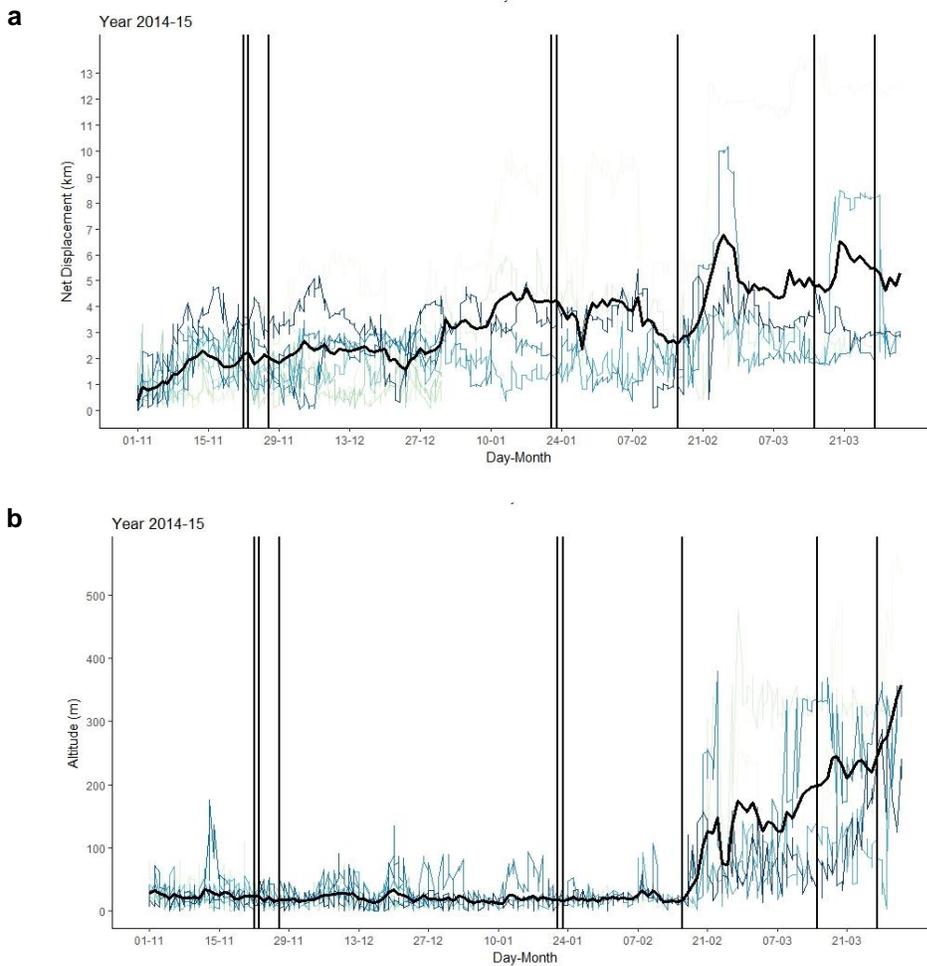
Fig. 15. During the winter of 2014-15 several rain-on-snow events occurred (marked by black vertical lines) on Kaffiøyra (weather data from Ny-Ålesund weather station). Here we show, from November 1 to March 31; *a)* the net displacement (km; upper graph) and *b)* altitude (masl. lower graph) of the nine GPS marked individuals in Kaffiøyra at that time. The black bold line indicates the mean net displacement and altitude across animals. The coloured lines shows responses of each individual female.

3.4.3 Behavioural responses to ground ice: Moving to better ranges

Studies using VHF and GPS collars on Svalbard reindeer have demonstrated the occurrence of partial seasonal migration, particularly under difficult winter foraging conditions (Hansen et al. 2010b, Stien et al. 2010). The early view that Svalbard reindeer are confined to small, year-round individual home ranges (Tyler and Øritsland 1989) has been nuanced after GPS-collars were mounted on female reindeer on Nordenskiöld Land (RSC since 2009) and along the west-coast (BSK since 2014). On Nordenskiöld Land, Loe and colleagues (2016) documented that individual range displacement occurred mainly during icy winters from valleys with ground ice to valleys with less ground ice. Compared with individuals staying behind in the icy valley, this movement strategy apparently resulted in lower over-winter loss of body mass, lower mortality rate, and higher subsequent fecundity. Meland (2014) estimated that up to 41 % of the GPS marked females used this strategy in the inland study area.

Around the millennium, when fjord ice was still largely present in winter in the coastal study area region, up to 35 % of female reindeer left their home range (i.e. calving grounds) on Brøgger Peninsula for better winter foraging conditions at Sarsøyra, likely crossing the fjord ice in Engelskbukta. Recently, however, fjord ice has been absent in the area, and data from GPS-collared reindeer since 2014 suggest that such migration patterns no longer occur. Based on the information from the GPS animals it appears that most animals use large parts of the peninsula as their annual winter range (Fig. 10). For instance Kvadehuken, which is a polar desert with very little accumulation of snow due to wind drift (Fig. 16), appears to be an area that is important winter foraging grounds. In the winter of 2015/16, six out of nine GPS marked animals used this location. This may represent another example, as well as utilizing the seashore and/or high-elevation feeding, of how animals with restricted dispersal opportunities adjust to and cope with difficult foraging conditions on small spatial scales. Accordingly, the home ranges will likely differ in size as well as geographic location among years, according to the amount of ice and snow in the terrain, as Kinck (2014) observed on Nordenskiöld Land. However, additional years of data are needed before we can relate home range sizes to annual feeding conditions statistically. The role of snow-pack depth and hardness (besides the ground ice layer) should be considered in such evaluations.

The lack of possibilities to move between peninsulas due to absence of fjord ice may represent a population-genetic challenge (e.g. to maintain genetic diversity at a population level). A population-genetic study (Peeters et al., unpublished), thus suggests significant genetic differentiation even between these nearby peninsulas (within BSK). In such small populations, the lack of possibilities to move to better foraging grounds in response to particularly icy winters could therefore have major eco-evolutionary effects in the long-term perspective. Small isolated populations are also much less robust to environmental stochasticity (e.g. extreme events) and thus more vulnerable to extinction.

Although movement between peninsulas are restricted, we observed some clear patterns of common movements within the peninsulas during this study and during the annual population censuses. For instance, individuals occasionally aggregate in spatially restricted ice-free hotspots in the lowlands, likely using their fine-tuned sense of smell to locate ice-free microhabitat beneath the snowpack (Hansen et al. 2010a). During the annual winter count in 2012, ~ 60 individuals (i.e. ca. one third of the total population) in Sarsøyra were gathered within a very small (0.1 km^2) area (Pedersen and Hansen, pers. obs.), and up to 15-20 % of the population has been observed in the south-facing bird-cliffs of Simlestupet, Brøgger Peninsula (Pedersen and Beumer pers. obs. 2017; Pedersen and Samuelsson pers. obs. 2018).

Fig. 16. *Kvadehuken, Brøgger Peninsula, is characterized as a polar desert interspersed by small spots with sparse vegetation. Kvadehuken appears to be especially important in winter because ground ice is less frequent in this wind-blown area.*

4 Concluding remarks

This report presents the first preliminary results from a four-year capture–mark–recapture study of coastal Svalbard reindeer females. We compare findings from our study with inland reindeer populations on Nordenskiöld Land, and summarize current knowledge on Svalbard reindeer spatial winter ecology. The project has improved our knowledge of the spatial ecology and behavioural responses to winter climate change in isolated, coastal populations of Svalbard reindeer, thereby contributing with essential information to the overall knowledge base available for management. We recommend continued monitoring of contrasting populations of this endemic sub-species.

Box 1. Project goals.

1. How does absence/presence of fjord ice and ground ice affect body condition, reproduction and spatial behaviour of female reindeer?
2. Can behavioural adjustments counteract climate impacts on forage availability?
3. What triggers and limits female reindeer movement patterns and thereby their spatial distribution?
4. What are the environmental factors driving the different reindeer population trends in Svalbard?

On Brøgger Peninsula on the west coast, there has been a negative population trend since the 1990s due to increasingly frequent rainy and icy winters. In contrast, a positive population trend has been evident in central Spitsbergen, which is a less rainy and icy region with a striking greening effect due to a warmer and longer snow-free season. In this project, we have shown that these contrasting trends are also reflected in the spatial ecology and opportunities to adapt to winter climate change. Several spatial restrictions likely contribute to the finding that home ranges are smaller in the coastal study populations than in the inland populations. The recent lack of sea ice combined with landscape barriers, such as tidewater glaciers and alpine mountains, restrict the dispersal opportunities. This represents a substantial challenge for individual reindeer, as ground icing triggers an immediate need for increased movement rates and search for better feeding grounds. Not surprisingly in the absence of fjord ice, we found that none of our GPS-collared female reindeer moved among the three study peninsulas, in sharp contrast to the movement patterns observed two decades ago, when fjord-ice was relatively frequent. However, we find that reindeer inhabiting these isolated peninsulas respond to poor winter-feeding conditions by other means of adjusting their foraging ecology. Feeding on kelp at the sea-shore and climbing to high elevations may contribute to buffer against negative fitness consequences of winter climate change, but the strategy of performing partial seasonal migration events among peninsulas in search for better feeding grounds, does not occur anymore. We therefore conclude that such increased isolation of coastal sub-populations may make them less robust to extreme stochastic events, with increased population-genetic challenges related to isolation.

Our study has demonstrated the importance of (1) using GPS collaring as a mean to monitor behavioural responses to climate change, and (2) monitoring several contrasting populations, both coastal and inland, simultaneously, as their responses are different. Because negative effects of winter warming are indeed evident in some coastal populations, it is of utmost importance for the management to continue the studies of reindeer spatial ecology and fitness variation in these isolated areas as climate change progresses. The management value is further increased by the integration of individual-based studies with long-term population monitoring data, and by comparing results with inland populations further south, where the climatic drivers and their effects on population growth differ (Hansen et al. unpublished). The implementation of the *Climate-ecological Observatory for Arctic Tundra* (COAT) is essential in this respect to monitor both short and long-term consequences of weather variability and climate changes on Svalbard reindeer populations, demographic structure and their spatial ecology.

Capture–mark–recapture studies are important for understanding reindeer responses to climate change. Currently, COAT facilitate such studies in both long-term population monitoring regions in Nordenskiöld Land and on the west coast of Svalbard. Photo: Erik Ropstad.

5 Literature

Aanes, R., B. E. Saether, and N. A. Oritsland. 2000. Fluctuations of an introduced population of Svalbard reindeer: the effects of density dependence and climatic variation. Ecography **23**:437-443.

Aanes, R., B. E. Saether, E. J. Solberg, S. Aanes, O. Strand, and N. A. Oritsland. 2003. Synchrony in Svalbard reindeer population dynamics. Canadian Journal of Zoology-Revue Canadienne De Zoologie **81**:103-110.

Albon, S. D., R. J. Irvine, O. Halvorsen, R. Langvatn, L. E. Loe, E. Ropstad, V. Veiberg, R. Van Der Wal, E. M. Bjorkvoll, E. I. Duff, B. B. Hansen, A. M. Lee, T. Tveraa, and A. Stien. 2017. Contrasting effects of summer and winter warming on body mass explain population dynamics in a food-limited Arctic herbivore. Global Change Biology **23**:1374-1389.

Beumer, L. T., O. Varpe, and B. B. Hansen. 2017. Cratering behaviour and faecal C:N ratio in relation to seasonal snowpack characteristics in a High-Arctic ungulate. Polar Research **36**:1, 1286121.

Bjorkvoll, E., B. Pedersen, H. Hytteborn, I. S. Jonsdottir, and R. Langvatn. 2009. Seasonal and Interannual Dietary Variation during Winter in Female Svalbard Reindeer *(Rangifer tarandus platyrhynchus).* Arctic Antarctic and Alpine Research **41**:88-96.

CAFF. 2010. Wild reindeer and caribou. Arctic Biodiversity Trends.

Calenge, C. 2006. The package "adehabitat" for the R software: A tool for the analysis of space and habitat use by animals. Ecological Modelling **197**:516-519.

Derocher, A. E., O. Wiig, and G. Bangjord. 2000. Predation of Svalbard reindeer by polar bears. Polar Biology **23**:675-678.

Governor of Svalbard. 2009. Plan for forvaltning av svalbardrein, kunnskaps- og forvaltningsstatus. Rapport 1/2009 (in Norwegian).

Eide, N. E., P. M. Eid, P. Prestrud, and J. E. Swenson. 2005. Dietary responses of arctic foxes *Alopex lagopus* to changing prey availability across an Arctic landscape. Wildlife Biology **11**:109-121.

Eide, N. E., A. Stien, P. Prestrud, N. G. Yoccoz, and E. Fuglei. 2012. Reproductive responses to spatial and temporal prey availability in a coastal Arctic fox population. Journal of Animal Ecology **81**:640-648.

Hansen, B. B., and R. Aanes. 2012. Kelp and seaweed feeding by High-Arctic wild reindeer under extreme winter conditions. Polar Research **31**:1-6.

Hansen, B. B., R. Aanes, I. Herfindal, J. Kohler, and B. E. Sæther. 2011. Climate, icing, and wild arctic reindeer: past relationships and future prospects. Ecology **92**:1917-1923.

Hansen, B. B., R. Aanes, I. Herfindal, B. E. Saether, and S. Henriksen. 2009. Winter habitat-space use in a large arctic herbivore facing contrasting forage abundance. Polar Biology **32**:971-984.

Hansen, B. B., R. Aanes, and B. E. Saether. 2010a. Feeding-crater selection by high-arctic reindeer facing ice-blocked pastures. Canadian Journal of Zoology **88**:170-177.

Hansen, B. B., R. Aanes, and B. E. Saether. 2010b. Partial seasonal migration in high-arctic Svalbard reindeer *(Rangifer tarandus platyrhynchus).* Canadian Journal of Zoology **88**:1202-1209.

Hansen, B. B., V. Grøtan, R. Aanes, B. E. Sæther, A. Stien, E. Fuglei, R. A. Ims, N. G. Yoccoz, and Å. Ø. Pedersen. 2013. Climate events synchronize the dynamics of a resident vertebrate community in the High Arctic. Science **339**:313-315.

Isaksen, K., O. Nordli, E. J. Forland, E. Lupikasza, S. Eastwood, and T. Niedzwiedz. 2016. Recent warming on Spitsbergen. Influence of atmospheric circulation and sea ice cover. Journal of Geophysical Research-Atmospheres **121**:11913-11931.

Iversen, M., J. Aars, T. Haug, I. Alsos, C. Lydersen, L. Bachmann, and K. M. Kovacs. 2013. The diet of polar bears *(Ursus maritimus*) from Svalbard, Norway, inferred from scat analysis. Polar Biology **36**.

Johansen, B. E., S. R. Karlsen, and H. Tommervik. 2012. Vegetation mapping of Svalbard utilising Landsat TM/ETM plus data. Polar Record **48**:47-63.

Kinck, C. 2014. Reduced forage access affects home range size and site fidelity of Svalbard Reindeer *(Rangifer tarandus platyrhynchus).* Master Thesis, Norwegian University of Life Sciences.

Kohler, J., and R. Aanes. 2004. Effect of winter snow and ground-icing on a Svalbard reindeer population: Results of a simple snowpack model. Arctic Antarctic and Alpine Research **36**:333-341.

Kolloen, M. R. 2015. Effects of weather on summer and winter activity level of the high arctic ungulate Svalbard reindeer *(Rangifer tarandus platyrhynchus).* Master Thesis, Norwegian University of Life Sciences.

Leader-Williams, N. 1980. Population-dynamics and mortality of reindeer introduced into south georgia. Journal of Wildlife Management **44**:640-657.

Loe, L. E., B. B. Hansen, A. Stien, S. D. Albon, R. Bischof, A. Carlsson, R. J. Irvine, M. Meland, I. M. Rivrud, E. Ropstad, V. Veiberg, and A. Mysterud. 2016. Behavioral buffering of extreme weather events in a high-Arctic herbivore. Ecosphere **7**.(6):e01374.

Lønø, O. 1959. Reinen på Svalbard. Norsk Polarinstitutt Meddelelse 83.

Meland, M. 2014. Partial migration as a response to ground icing events in a high arctic ungulate. Master Thesis, Norwegian University of Life Sciences.

Meltofte, H. 2013. Arctic Biodiversity Assessment. Status and trends in Arctic biodiversity. Conservation of Arctic Flora and Fauna, Akureyri.

Movik, L. K. 2018. Effects of spatio-temporal weather conditions in autumn and winter on body mass and behaviour of the high Arctic Svalbard reindeer *(Rangifer tarandus platyrhynchus).* Master Thesis, Norwegian University of Life Sciences.

Muckenhuber, S., F. Nilsen, A. Korosov, and S. Sandven. 2016. Sea ice cover in Isfjorden and Hornsund, Svalbard (2000-2014) from remote sensing data. Cryosphere **10**:149-158.

Nedberg, T. 2012. The effect of ground icing events on Svalbard reindeer *(Rangifer tarandus platyrhynchus)* space use and habitat selection. Master Thesis, Norwegian University of Life Sciences.

Pedersen, Å. Ø., B. J. Bårdsen, V. Veiberg, and B. B. Hansen. 2014. Jegernes egne data. Analyser av jaktstatistikk og kjevemateriale fra svalbardrein. Norsk Polarinstitutt Kortrapport 27.

Putkonen, J., and G. Roe. 2003. Rain-on-snow events impact soil temperatures and affect ungulate survival. Geophysical Research Letters **30**.

Reimers, E. 1977. Population dynamics in two subpopulations of reindeer in Svalbard. Arctic and Alpine Research **9**:369-381.

Rennert, K. J., G. Roe, J. Putkonen, and C. M. Bitz. 2009. Soil thermal and ecological impacts of rain on snow events in the circumpolar Arctic. Journal of Climate **22**:2302-2315.

Solberg, E. J., P. Jordhoy, O. Strand, R. Aanes, A. Loison, B. E. Sæther, and J. D. C. Linnell. 2001. Effects of density-dependence and climate on the dynamics of a Svalbard reindeer population. Ecography **24**:441-451.

Stien, A., R. A. Ims, S. D. Albon, E. Fuglei, R. J. Irvine, E. Ropstad, O. Halvorsen, L. E. Loe, V. Veiberg, and N. G. Yoccoz. 2012. Congruent responses to weather variability in high arctic herbivores. Biology Letters **8**:1002-1005.

Stien, A., R. J. Irvine, E. Ropstad, O. Halvorsen, R. Langvatn, and S. D. Albon. 2002. The impact of gastrointestinal nematodes on wild reindeer: experimental and cross-sectional studies. Journal of Animal Ecology **71**:937-945.

Stien, A., L. E. Loe, A. Mysterud, T. Severinsen, J. Kohler, and R. Langvatn. 2010. Icing events trigger range displacement in a high-arctic ungulate. Ecology **91**:915-920.

Tyler, N. J. C., M. C. Forchhammer, and N. A. Oritsland. 2008. Nonlinear effects of climate and density in the dynamics of a fluctuating population of reindeer. Ecology **89**:1675-1686.

Tyler, N. J. C., and N. A. Øritsland. 1989. Why dont svalbard reindeer migrate. Holarctic Ecology **12**:369-376.

van der Wal, R. 2006. Do herbivores cause habitat degradation or vegetation state transition? Evidence from the tundra. Oikos **114**:177-186.

van der Wal, R., R. D. Bardgett, K. A. Harrison, and A. Stien. 2004. Vertebrate herbivores and ecosystem control: cascading effects of faeces on tundra ecosystems. Ecography **27**:242-252.

van der Wal, R., and A. Stien. 2014. High arctic plants like it hot: a long term investigation of between-year variability in plant biomass across habitats and species. Ecology **95**:3414–3427.

Veiberg, V., L. E. Loe, S. D. Albon, R. J. Irvine, T. Tveraa, E. Ropstad, and A. Stien. 2017. Maternal winter body mass and not spring phenology determine annual calf production in an Arctic herbivore. Oikos **126**:980-987.

Vickers, H., K. A. Hogda, S. Solbo, S. R. Karlsen, H. Tommervik, R. Aanes, and B. B. Hansen. 2016. Changes in greening in the high Arctic: insights from a 30 year AVHRR max NDVI dataset for Svalbard. Environmental Research Letters **11**.

Zuur, A. F., E. N. Ieno, N. J. Walker, A. A. Saveliev, and G. M. Smirth. 2009. Mixed effect models and extensions in ecology with R.:574.